A NEW MUSSEL (BIVALVIA, MYTILIDAE) FROM HYDROTHERMAL VENTS IN THE GALAPAGOS RIFT ZONE

Vida Carmen Kenk[1] & Barry R. Wilson[2]

ABSTRACT

A new subfamily, Bathymodiolinae, and new genus and species, *Bathymodiolus thermophilus,* are described from material collected by the 1977 and 1979 expeditions to the hydrothermal vents in the Galapagos Rift Zone. This large modioliform mussel has very unusual anatomy, exhibiting extreme mantle fusion which restricts the incurrent aperture to a short byssal-pedal gape in the ventral midregion. The gills lack food grooves ventrally; the free edges of the gills fit axial ridges on the visceral mass and mantle lobes, thereby isolating the dorsal excurrent chambers from the rest of the mantle cavity. The gut is short and different from that of other mytilids in lacking a recurrent loop, the stomach is simple and lacks a deep sorting caecum, dorsal hood and left pouch, and there are but three pairs of digestive ducts opening into the stomach. The auricles of the heart have a broad connection to the longitudinal vein laterally between the branches of the divided posterior retractor muscles in addition to the normal connection anterior to these muscles. The kidney is very small.

Feeding is discussed in light of high densities of chemoautotrophic sulphur-oxidizing bacteria in the environment and the possibility of a symbiotic relationship between the mussels and bacteria.

INTRODUCTION

The discovery in 1977 of biological communities surrounding hydrothermal vents in the Galapagos Rift Zone at latitude 00.47°N (Corliss & Ballard, 1977; Lonsdale, 1977; Corliss *et al.,* 1979; Enright *et al.,* 1981; Edmond, 1982) led to the Galapagos Rift Biology Expedition in 1979 (Ballard & Grassle, 1979; Galápagos Biology Expedition Participants, 1979). Since the initial discovery, additional submarine hydrothermal communities have been described at 21°N (Rise Project Group, 1980) and 11–13°N (Desbruyères *et al.,* 1982). The majority of specimens collected on these expeditions are unusual organisms differing from known relatives at generic or higher levels (Newman, 1979; Williams, 1980; Burreson, 1981; Fretter *et al.,* 1981; Jones, 1981; Krantz, 1981; McLean, 1981; Desbruyères & Laubier,1982; Williams & Chace, 1982).

One of the most abundant and conspicuous organisms collected at some of these hydrothermal vents is a large modioliform mussel. Although the shell form is like that of the mytilid genus *Modiolus,* anatomical study of preserved specimens has revealed many dis-

tinctive features. This animal is described here as a new genus and species and a new subfamily is erected for it. The mussels were abundant at several vent sites in the Galapagos Rift Zone. The species is also present, though apparently less abundantly, at the 11–13°N site, but was not collected or observed at the vents at 21°N.

MATERIALS AND METHODS

All of the specimens examined in this study were from the Galapagos Rift Zone vents, viz.:

a) 79 specimens preserved in ethanol (size range 0.3 to 14.38 cm in length) collected during the 1977 expedition at Clambake 1, Oyster Bed, and Garden of Eden vent sites (dive stations 713, 723, 727, 728 and 733) and forwarded to the authors by Dr. Jack Corliss.

b) 11 specimens preserved in ethanol (size range 7.9 to 16.2 cm) collected during the 1979 expedition at Rose Garden and Mussel Bed vent sites (dive stations 879, 880, 894 and 896) and forwarded to the authors by Dr. Fred Grassle, and 153 juveniles

[1]Department of Biological Sciences, San Jose State University, San Jose, CA 95192 U.S.A.
[2]Museum of Victoria, Division of Natural History and Anthropology, 285-321 Russell St., Melbourne, Victoria 3000, Australia. New address: Dept. Conservation & Land Management, Matilda Bay, Nedlands, Western Australia 6009. Australia.
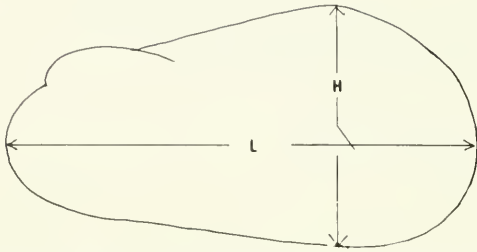
FIG. 1. Diagram indicating the measurement taken for length and height. Width is greatest dimension through both valves.

(size range 0.3 to 9.8 mm) collected from washing of mussels from dives 880 and 884, loaned by Dr. Howard Sanders.

c) 75 dried shells deposited at the U.S.N.M., lot registration number 81331600-3380-P30000.

Seven preserved specimens from sample a) were dissected under a binocular microscope. Anatomical drawings were done freehand; shells were drawn with the aid of a camera lucida. Measurements taken are illustrated in Fig. 1.

The holotype and a large series of paratypes are lodged at the U.S.N.M. Paratypes are also lodged at the following museums: California Academy of Sciences, San Francisco; Museum of Comparative Zoology, Harvard University; Los Angeles County Museum; British Museum of Natural History, London; Museum National d'Histoire Naturelle, Paris; Museum of Victoria, Melbourne; Zoologisk Museum, University of Copenhagen; Academy of Natural Sciences, Philadelphia; Scripps Institute of Oceanography.

KEY TO ABBREVIATIONS
IN FIGURES

AA, aa	anterior adductor muscle
a art	anterior artery
aff v	afferent vein
a l	ascending lamella
an	anus
AR, ar	anterior retractor muscle
au	auricle
b	byssus
bg	byssal gland
b-p g	byssal-pedal gape
b s	branchial septum
cb	connecting bar
d c d s	dorsal cul de sac
d d	digestive duct
d l	descending lamella
eff v	efferent vein
ex s	excurrent siphon
f	foot
f g	food groove
g ax	gill axis
g s	gastric shield position
gen ap	genital aperture
gen d	anterior genital duct
i	intestine
i ch	incurrent chamber
i d	internal diaphragm
i dem	inner demibranch
i ex ch	inner excurrent chamber
i g	intestinal groove
i m f	inner mantle fold
k	kidney
l p	labial palp
LPM	labial palp muscle
l v	longitudinal vein
m t	major typhlosole
mth	mouth
o	oesophagus
o dem	outer demibranch
o ex ch	outer excurrent chamber
o g	oral groove
o m f	outer mantle fold
p	papilla
PA, pa	posterior adductor muscle
pbr(a), APR	posterior byssal retractor muscle (anterior)
pbr(p), PPR	posterior byssal retractor muscle (posterior)
per	pericardium
PL	pallial line
pm	pallial muscles
ppr	posterior pedal retractor muscle
r	rectum
r ap	renal aperture
rg	ridge for gill attachment
r p c	reno-pericardial channel
s	septum of principal filament
SR, sr	siphonal retractor muscles
st	stomach
st a	stomach anterior chamber
st p	stomach posterior chamber
s v-au p	secondary venous-auricular passage
v	ventricle
v s m	valvular siphonal membrane

TAXONOMY

Family MYTILIDAE

BATHYMODIOLINAE
Kenk & Wilson, subfam. nov.

Type-genus: *Bathymodiolus*
Kenk & Wilson, gen. nov.

BATHYMODIOLUS
Kenk & Wilson gen. nov.[3]

Type-species: *Bathymodiolus thermophilus*
Kenk & Wilson, sp. nov.[3]

Diagnosis of the subfamily and genus:

Shell smooth, modioliform, with sub-terminal umbones; hinge edentulous; periostracum hirsute; posterior retractor muscle divided, retractor scars separate; pallial muscles including siphonal retractors strong; excurrent siphon short, extensible, with internal diaphragm; inner folds of the mantle lobes enlarged, extensible postero-ventrally, fused in the mid-line antero-ventrally and postero-ventrally; auricles enlarged, fused posteriorly; gills heterorhabdic, eleutherorhabdic, with short, fleshy filaments, lacking food grooves at ventral edges of demibranchs; with tubular connections present posteriorly between free edges of ascending lamellae and gill axes; labial palps small; stomach without a deep sorting caecum or left pouch; intestine short, lacking a recurrent loop.

Bathymodiolus thermophilus
Kenk & Wilson, sp. nov.

Type-locality: lat. 00°47'.89"N; long. 086°09'.21"W. Depth 2495 m. R/V *Alvin* Dive 879, at "Mussel Bed" geothermal vent, Galapagos Rift. *Holotype* (Fig. 2.): USNM 803661, preserved in 70% ethanol. Collected 20 January 1979 by Ellis and Ballard on *Alvin*. Measurements: length 14.95 cm, height 6.30 cm, width 5.83 cm (Fig. 2).

---

[3]In a paper on a similar or identical mussel from the East Pacific Rise at 11°–13°N, Le Pennec *et al.* (1984: 70) introduced *Bathymodiolus* as a *nomen nudum*. Also, the generic name has been used repeatedly in a popular article by Laubier & Desbruyères (1984); the manuscript species name *B. thermophilis* [sic] appeared on p.1510. Information in the former paper unfortunately was not considered by the authors of the present paper. ED.

DESCRIPTION

Shell morphology. Modioliform, solid, elliptical in juveniles and subadults, arcuate in old specimens, equivalve. Anterior end rounded; dorsal margin slightly convex; postero-dorsal corner rounded in adults, angular in juveniles; posterior end rounded; ventral margin nearly straight in specimens less than 10 cm length, slightly concave in larger specimens (Fig. 3). Umbones subterminal, prosogyrate.

External surface smooth, sculpture lacking, dull white beneath periostracum. Interior white, nacreous. Periostracum straw-yellow, yellow-brown antero-ventrally, often stained dark brown in large specimens. In young specimens less than 0.8 cm in length periostracum smooth, larger juveniles develop periostracal hairs (of byssal origin, see Bottjer & Carter, 1980; Ockelmann, 1983) on posterior slope; specimens more than 2 cm long have hairs on most of shell exterior; hairs broad, flat. In addition to their own hairs many shells bear byssal end-plates of other mussels which had been attached to them, distinguishable by oval shape and central slender strand.

Ligament opisthodetic, parivincular, strong, extending most of length of dorsal margin; resilial ridge (as defined by Soot-Ryen, 1955: 7) deep, chalky and rather soft, not pitted; sub-ligamental shell ridge strong and angular, with deep groove between it and ligament anteriorly, becoming obsolete below midpoint of ligament. Hinge edentulous except for strong backward pointing projection of anterior hinge margin beneath anterior end of ligament; post-ligamental denticles lacking.

Muscle scars (Fig. 4). Anterior adductor muscle scar half-moon shaped, located below umbo, distant from anterior margin (Fig. 4); young specimens may show small round scar of labial palp support muscles just behind anterior adductor; anterior byssal-pedal retractor scar oval, located high within umbonal cavity behind umbo; posterior adductor scar rounded-rectangular; posterior byssal-pedal retractor muscles form two separate scars with large gap between them, anterior one elongate-elliptical, located high, and close to posterior end of ligament, second one elliptical and located antero-dorsally to but contiguous with posterior adductor scar to form a joint comma-shaped scar. Pallial line distinct, extending ventrally from anterior adductor to posterior adductor, curving upwards to form
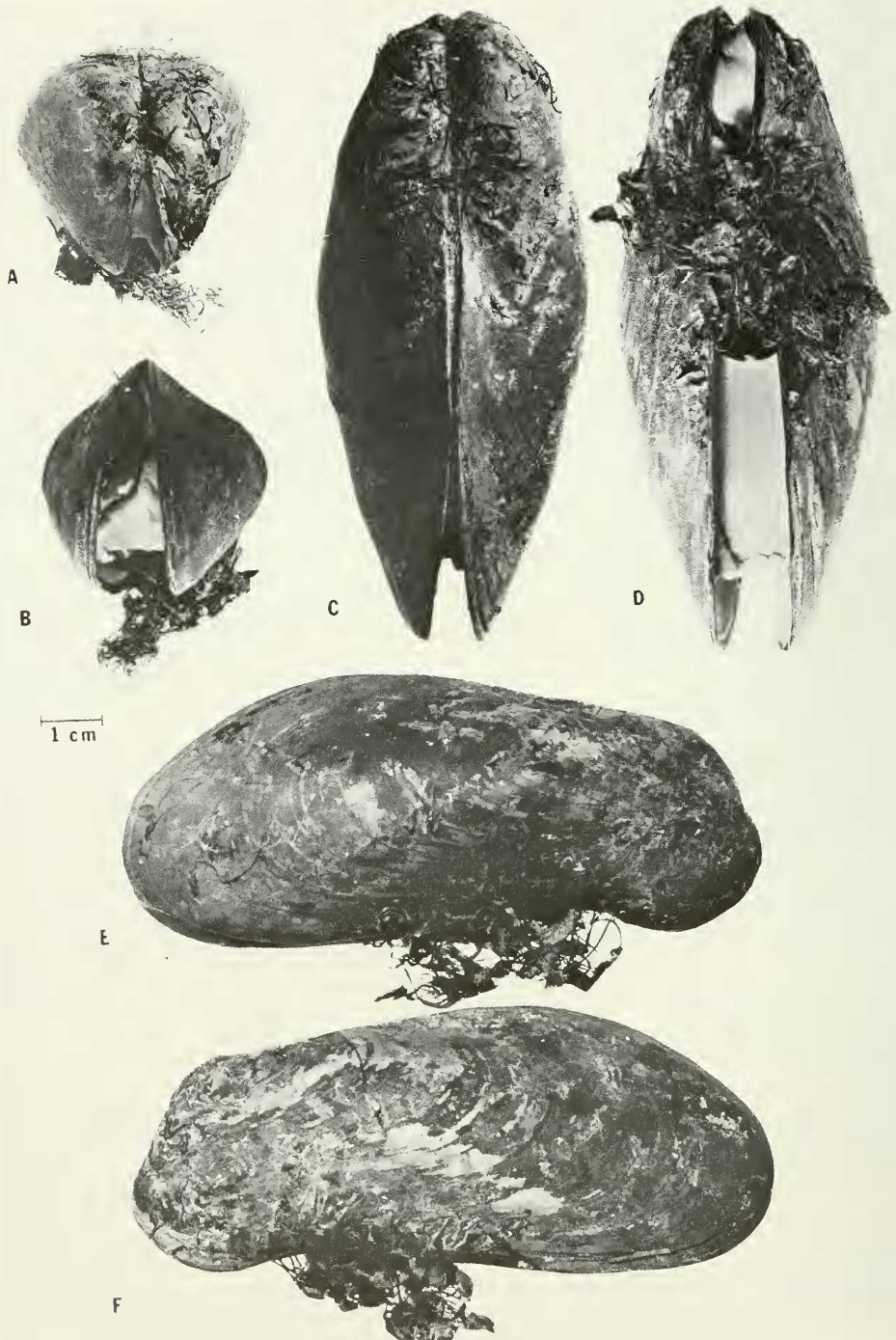
FIG. 2. *Bathymodiolus thermophilus*, holotype, USNM 803661. A, anterior view; B, posterior view; C, dorsal view; D, ventral view; E, lateral view, right valve; F, lateral view, left valve.
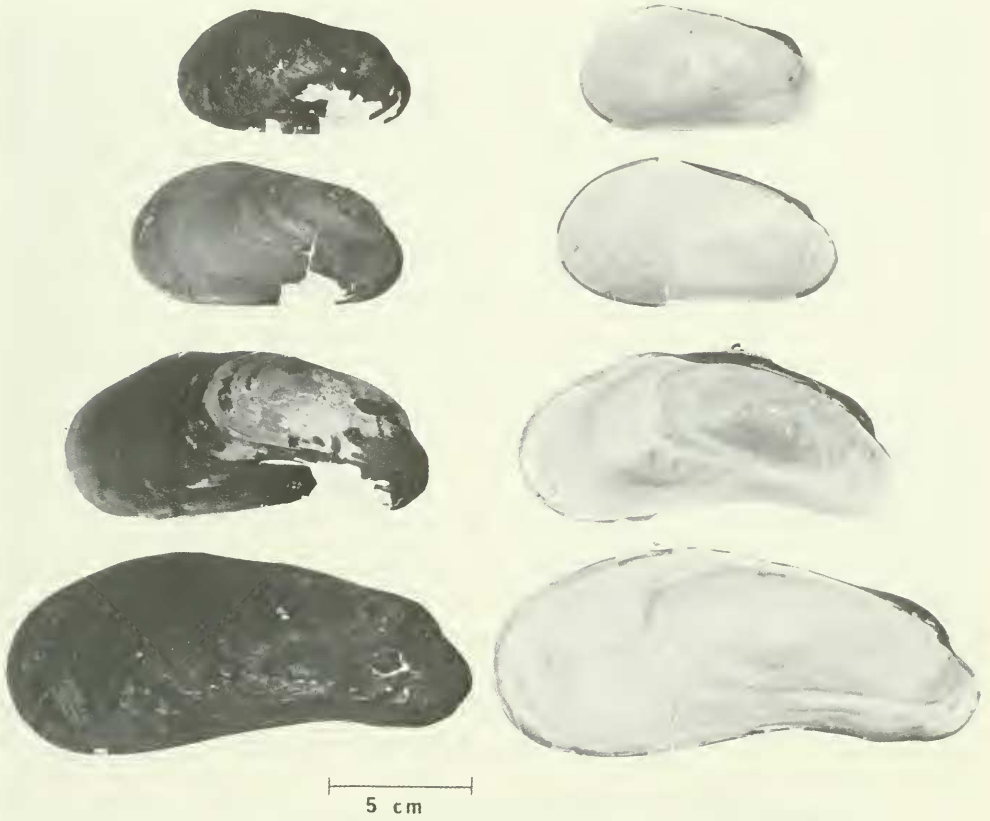
5 cm

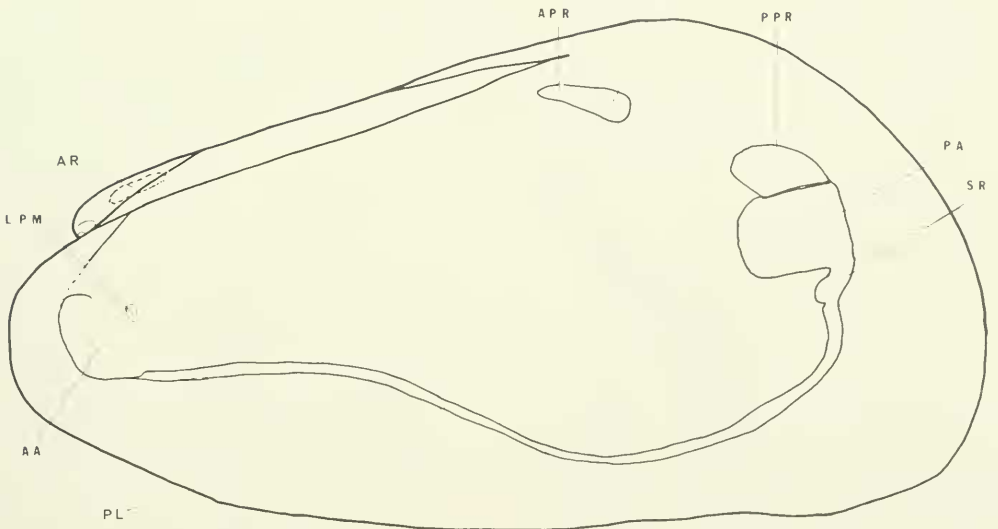FIG. 3. Growth series of shells illustrating change in form (paratypes, USNM 813316).

FIG. 4. Diagram of shell illustrating muscle scars.

concavity in byssal region about ⅓ of the distance from anterior end; small siphonal retractor scar present adjacent to posterior adductor scar at posterior end of pallial line.

Measurements. Rhoads *et al.* (1982) reported the largest shell in their series as 18.4 cm long. Maximum shell length observed in this study 16.3 cm. Length, height and width proportions of preserved specimens (paratype series, N = 79):

mean height/length 0.568; range 0.514 to 0.604
mean width/length 0.362; range 0.323 to 0.438

Anatomy

Musculature (Fig. 5). Main features of musculature evident from previous description of muscle scars. Posterior byssal retractors in two roughly equal main bundles arising together at base of byssus but diverge and attach separately to shell. Posterior pedal retractors thick, arising from base of foot anterior to origin of posterior byssal retractors, passing dorsally lateral to anterior retractors and inserting dorsally on both inner and outer

sides of most anterior bundles of posterior retractors.

Pallial muscles unusually well developed; strong siphonal retractors present, formed of amalgamated strands originating in inner mantle folds in region of excurrent siphon. Slender strand of anterior pedal retractor muscle extends anteriorly and attaches to shell behind anterior adductor, providing support for labial palps. Posterior adductor large and divided into "quick" and "catch" parts; anterior adductor elongate, half-moon shaped.

Foot and byssus (Fig. 5). Foot thick, flattened, terminally swollen; byssal groove running along ventral surface almost to tip. Byssus profuse, usually emerging as separate strands from orifice, strands thick and strong; byssal gland yellow, extends down centre of foot behind groove, without extension dorsal to anterior retractor muscles.

Mantle. Mantle lobes thin dorsally but become unusually thickened and muscular near posterior and ventral edges (Fig. 6). Free edges of mantle lobes have three folds as in other mytilids (Yonge, 1957); inner folds fuse
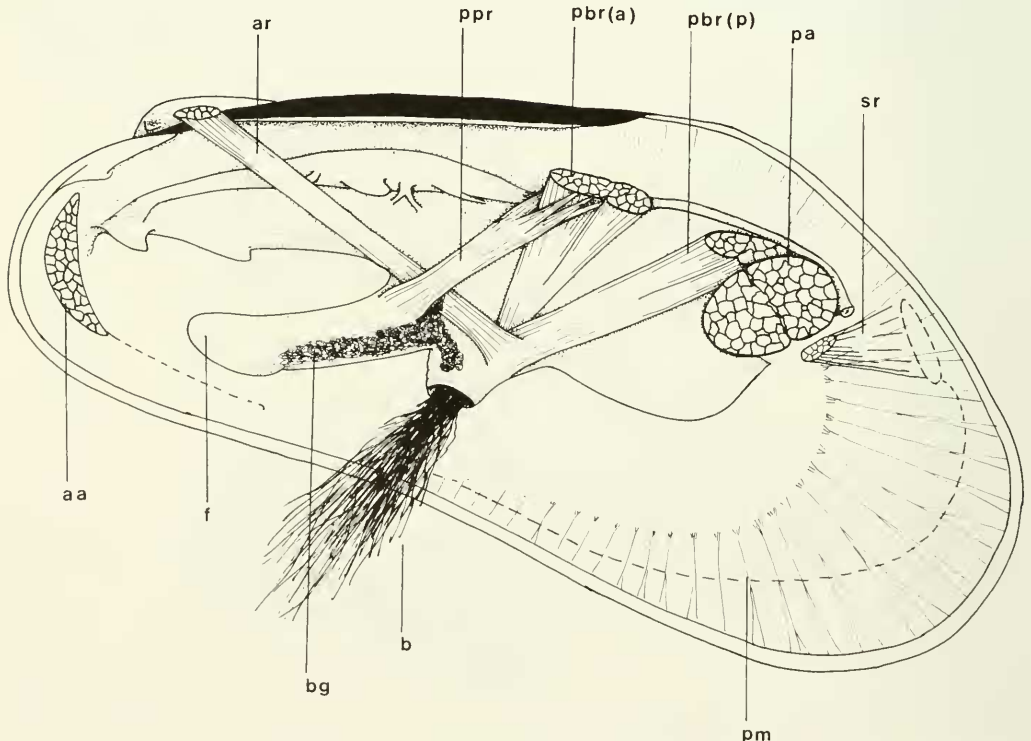

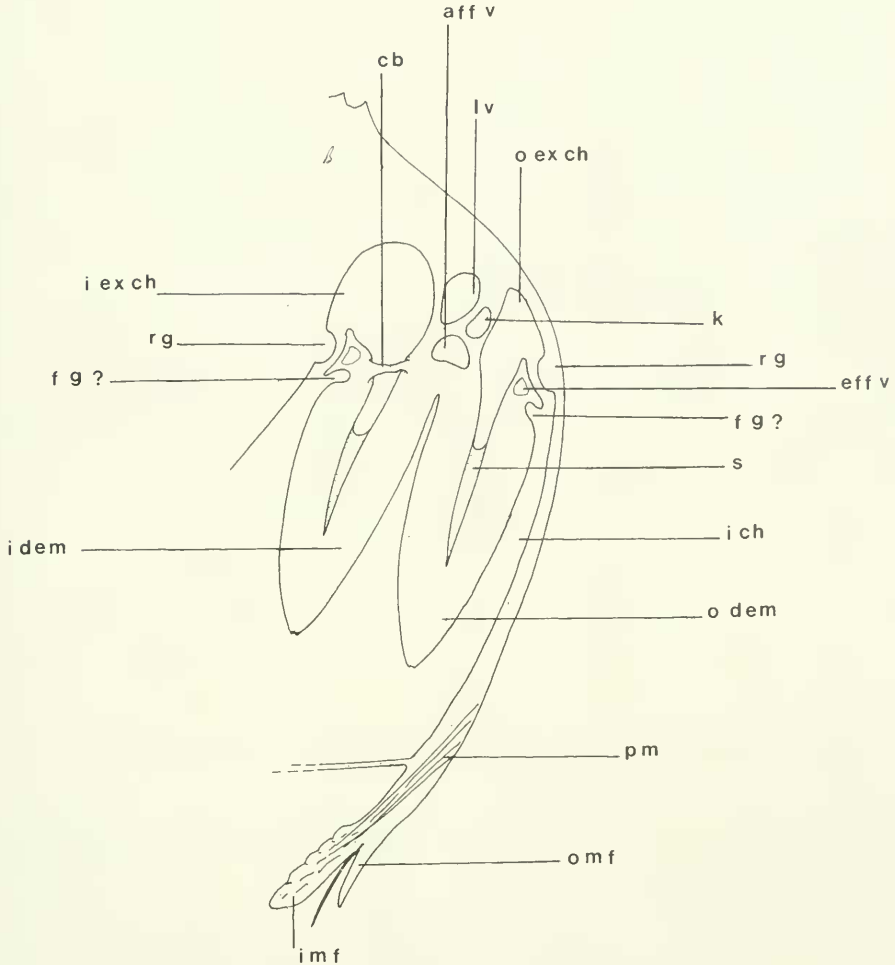FIG. 5. Musculature; left valve, mantle lobe and ctenidia removed.

FIG. 6. Transverse section of the right gills, through primary filaments and with one of several connecting bars between the free edge of the inner ascending lamella and the gill axis.

mesially along the entire postero-dorsal slope and ventrally enclosing the mantle cavity to an unusual extent.

Excurrent siphon formed posteriorly between inner folds, capable of moderate extension but shown in retracted position in Fig. 7; thin internal diaphragm with narrow horizontal aperture partly occludes inner end of excurrent siphon.

Fusion of inner mantle folds immediately below excurrent siphon forms horizontal shelf, the branchial septum, with an inner part reaching forward to ventral side of posterior adductor (Fig. 7). Branchial septum separates incurrent and excurrent chambers posteriorly; posterior ends of gill axes attach to its ventral surface. Ventral development of branchial septum forms an oblique, transverse partition, the valvular siphonal membrane (terminology of Yonge, 1955), joining left and right lobes postero-ventrally thus enclosing incurrent mantle cavity in that region; inner folds also fused in mid-line antero-ventrally; incurrent aperture thus confined to a short ventral pedal-byssal gape (Figs. 7, 8).

Rim of gape bordered by another muscular fold which may regulate aperture size by muscular contraction. A small papilla present at posterior end of gape (Fig. 8).

Free edges of inner folds form wide extensible frills postero-ventrally shown partly extended in Fig. 7. Fig. 12 shows them fully
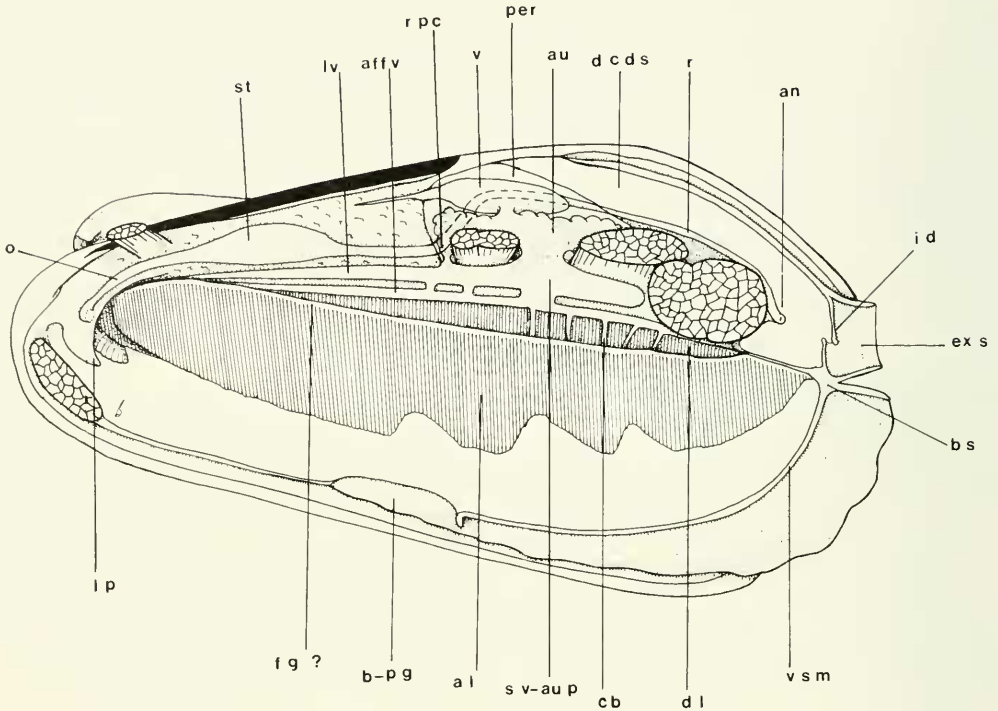
FIG. 7. Vascular and alimentary systems and siphonal structure; left valve and mantle lobe removed; fused inner mantle folds cut down the mid-line (in sagittal section). Outer demibranch deformed.

extended in life. This structure forms functional, though not tubular, incurrent siphon by apposition of edges ventrally. Excurrent and incurrent siphons separate as in *Botula* (Wilson & Tate, 1984).

Mantle cavity. Mantle cavity divided by ctenidia laterally and branchial septum posteriorly into ventral incurrent and dorsal excurrent chambers. Edges of ascending lamellae flanged and fitted to muscular longitudinal ridges on surfaces of mantle lobes and visceral mass thus completely separating incurrent and excurrent chambers in life (Fig. 6). In this way four tunnel-like, longitudinal excurrent chambers are formed along roof of mantle cavity, two on each side; chambers meet posteriorly at entrance of excurrent siphon above branchial septum.

A *cul de sac* of excurrent chamber passes posterodorsally above rectum and posterior adductor, reaching forward as far as posterior wall of pericardium (Fig. 7); thin pericardial wall separates pericardial fluids from sea water in excurrent mantle cavity.

Ctenidia. Paired ctenidia consist of inner and outer demibranchs each with descending and ascending lamellae forming W-shaped gill typical of mytilids (Fig. 6); demibranchs approximately equal-sized, inner demibranchs extend slightly further anteriorly, outer demibranchs slightly deeper; both demibranchs end abruptly anteriorly (Fig. 9). Ctenidia filibranchiate, heterorhabdic and eleutherorhabdic; interlamellar junctions lacking but every third to seventh filament is "principal filament" (see type B(1b) of Atkins, 1937, text fig. 4) with septum or "baffle" rising to more than half the height of gill (Fig. 6). Demibranchs rather short, filaments wide and fleshy; ventral edges lack food grooves though minute indentations present. Deep folds on outer surface of ascending lamellae just below free edges might function as food grooves; anteriorly folds continue in a loop as grooves on mantle wall and terminate in deep oral groove between labial palps leading into mouth.

Inter-lamellar tissue junctions lacking; series of about four large tubular connections present in posterior area between free edges and gill axes (Figs. 6, 10) appearing to connect efferent veins with either afferent or
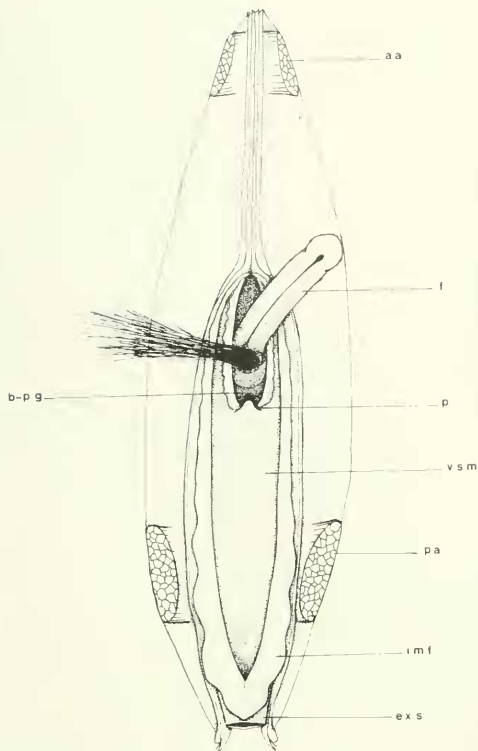
Fig. 8. External view from the ventral side (shell valves removed) showing extensive mid-line fusion of the inner mantle folds, the extended valvular siphonal membrane of the branchial septum and the small byssal-pedal gape.

longitudinal veins. Filaments sometimes thickened, shortened, deformed, particularly posteriorly, possibly due to activities of polychaetes.

Labial palps. Paired labial palps short, broad, flat, triangular; usually strongly plicate on their inner surfaces (Fig. 9); outer palps larger than inner palps and placed farther posteriorly, markedly so in some large specimens (e.g. Fig. 5). In very large specimens palps sometimes smooth, lacking plications on either surface.

Alimentary system. Digestive tract short, more or less straight, direct. Mouth transverse, slit-like; esophagus enters anterior end of stomach which lies superficially in visceral mass below ligament.

Stomach (Fig. 11; nomenclature of parts follows Reid, 1965) small elongate, divided into anterior and posterior chambers; backward-pointing pouch on left dorsal side of anterior chamber; posterior chamber swollen on right side, left pouch lacking; gastric shield small, located in normal position on anterodorsal wall on left side of posterior chamber. Three pairs of digestive ducts enter stomach laterally (Fig. 11) one pair on left and right sides of anterior chamber and two pairs on left and right side of posterior chamber; on right side two ducts open into posterior chamber close together; on left side two openings spaced apart with posterior one much the larger. Major typhlosole straight except for an elbow close to its entry into intestine, passes along floor of posterior chamber in mid-line and terminates in centre of anterior chamber; minor typhlosole branches on right side at elbow and passes up right side of posterior chamber (not traced further). Intestinal groove originates in opening of posterior digestive duct of left side and passes forward along floor of stomach to left of major typhlosole, passes around tip of that typhlosole in the anterior chamber, and returns down right side to enter intestine posteriorly. Surface of major typhlosole transversely plicate. Minor intestinal groove runs along anterior side of minor typhlosole on right side of posterior chamber but its origin not located. Hood groove not observed but this may have been a consequence of the poor preservation.

Style sac and intestine conjoined; crystalline style present in some preserved specimens. Intestine leaves posterior end of stomach and traverses short distance posteriorly down mid-line; rectum turns upwards to enter pericardium and ventricle from below; thence passes posteriorly through ventricle and directly down the mid-line to anus on posterior side of posterior adductor muscle; recurrent loop of intestine lacking.

Vascular system. Pericardium in usual position dorsally between posterior retractor muscles (Figs. 7, 12); broad reno-pericardial canal on each side passes laterally around most anterior of posterior retractor muscles, then ventrally to gill axis; canals superficial and easily seen when shell removed. Heart three-chambered (Fig. 12); medial ventricle thick, muscular, rhomboidal, traversed for much of its length by rectum; anteriorly ventral surface of ventricle fused to floor of pericardium. Paired anterior arteries arise from aortic bulb and pass forward over visceral mass; large ventral artery leads downwards through pericardial floor.

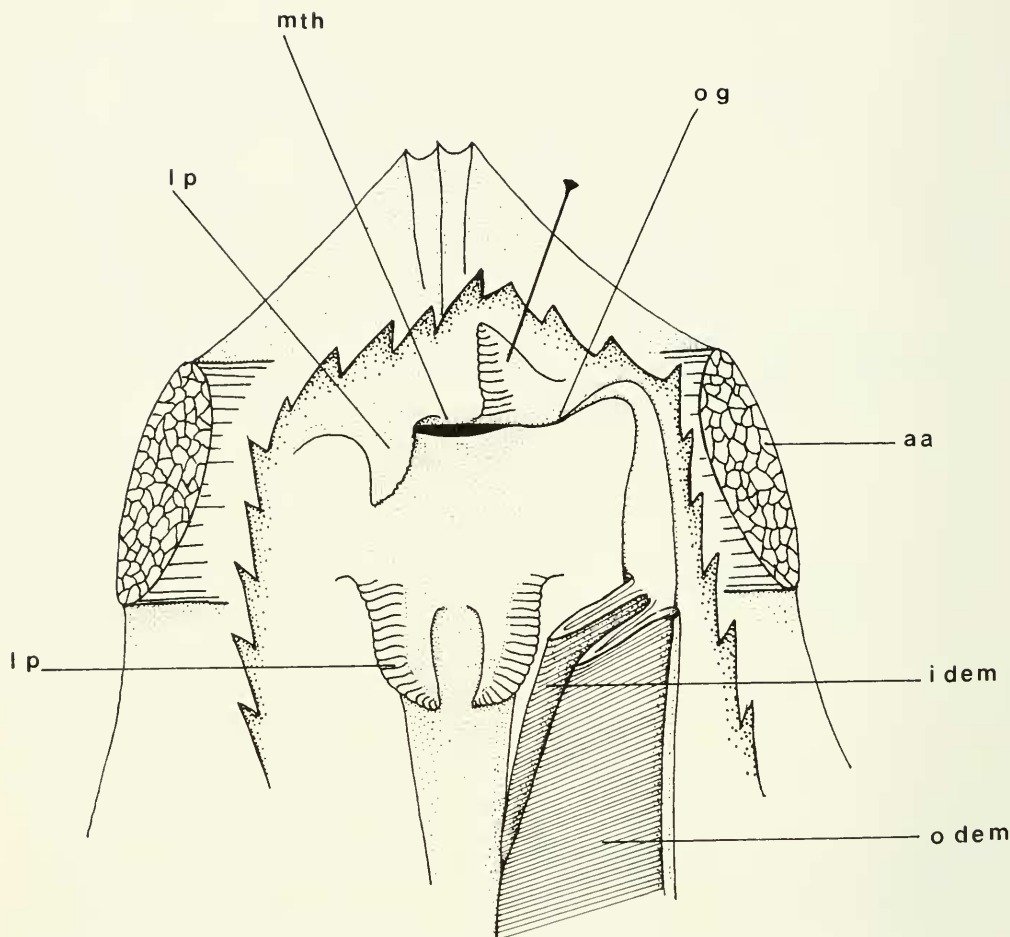Two auricles unusually large, fused together posteriorly (Fig. 12); each has an anterior arm

FIG. 9. Ventral view of the labial palps with the mantle and anterior adductor cut away; the inner palp of the left side is pinned back to expose the oral grooves.

curving laterally and downward within reno-pericardial canal but connection via oblique vein to longitudinal vein (see White, 1937, for description in *Mytilus*) not observed. Each auricle has wide latero-ventral flap protruding between bundles of posterior retractor muscles, with a wide foramen opening directly into longitudinal vein; valvular mechanism in that opening appears to be lacking.

Efferent veins in free edges of demibranchs, and afferent and longitudinal veins immediately above gill axis readily observable in hand-cut sections; longitudinal veins large and spacious in zone between reno-pericardial canal and posterior adductor. In dissections it appeared that there are several foramina between afferent and longitudinal veins in this zone; largest of these located

directly below wide space connecting longitudinal veins and latero-ventral flaps of auricles.

Plicate membranes lacking (see White, 1937 for details of these structures in *Mytilus* between visceral mass and gill axes and mantle lobes and gill axes).

Tubular junctions between free edges of demibranches and gill axes already noted; whether these are vascular connections needs to be determined.

Nervous system. Paired ganglia situated in normal positions, cerebral ganglia between anterior retractor muscles near attachment of inner labial palps; paired pedal ganglia medially just above region where anterior and posterior retractor muscles meet foot; paired visceral ganglia on ventral surface of posterior adductor muscle.
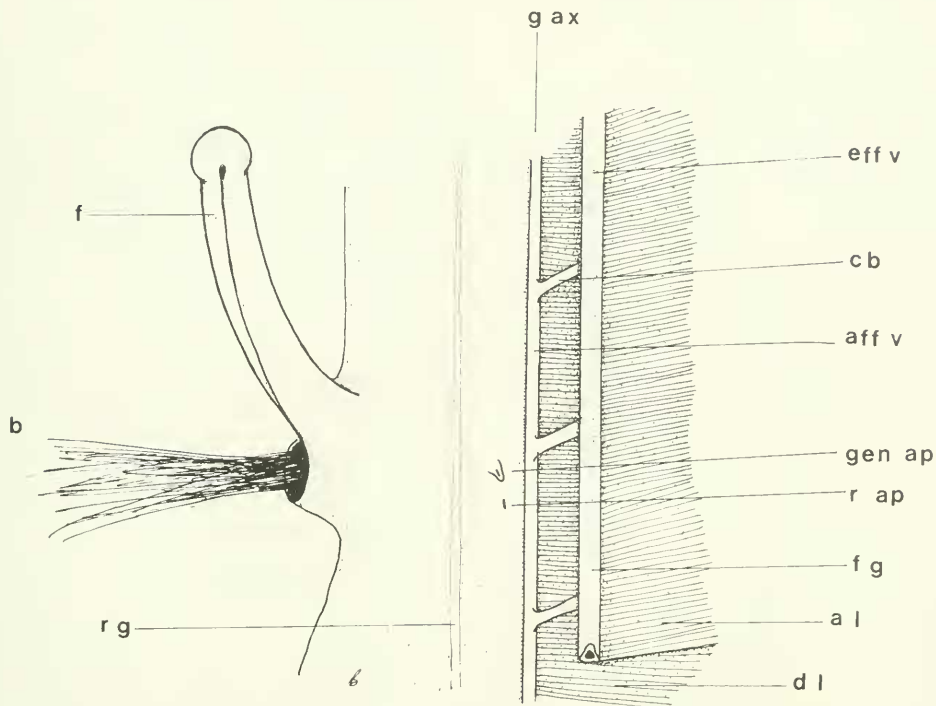
FIG. 10. Location of the genital and renal apertures, and showing the connecting bars between the gill axis and the free edge of the ascending lamella of the inner demibranch.

Reproductive system. In all large specimens examined gonad tubules were in regressed condition; confined to mesosoma and visceral mass over and behind digestive gland and below pericardium, lacking in mantle lobes. Genital apertures located at tips of very small conical papillae in roof of inner excurrent chambers at a point adjacent to byssus (Fig. 10).

Excretory system. In transverse hand-cut section taken through body below pericardium, a small axial duct closely associated with longitudinal vein was tentatively identified as kidney; duct very thin-walled and impossible to dissect out under the microscope, longitudinal extent of it, and whether or not it is recurved, could not be determined.

Renal apertures extremely small slits on slight protuberances in roof of inner excurrent chambers, just behind genital apertures (Fig. 10).

BIOLOGY

Life history and dispersal. The relatively ephemeral nature of a given active vent site and the distance between sites require an effective mechanism for dispersal if a species is to survive after a vent site becomes inactive. Lutz *et al.* (1980) examined the larval shell by scanning electron microscopy and found that prodissoconch I is small relative to the size of prodissoconch II. Comparisons they made with the larval shells of other mytilids such as *Mytilus edulis* and *Modiolus modiolus* suggest that *Bathymodiolus thermophilus* has long-lived planktonic larvae which could be transported from one vent site to another. The small size of prodissoconch I suggests very high fecundity. Lutz *et al.* (1980) proposed that these larvae may be induced to settle and undergo metamorphosis by encountering elevated temperatures at vent areas and might even delay metamorphosis in the absence of this stimulus.

Growth rates. Rhoads *et al.* (1981, 1982) derived growth rates from marked and recovered mussels at the "Mussel Bed" and "Rose Garden" sites and from recently settled young, which are among the highest recorded for deep-sea species. Mature mussels have mean growth rates of about 1 cm per year.
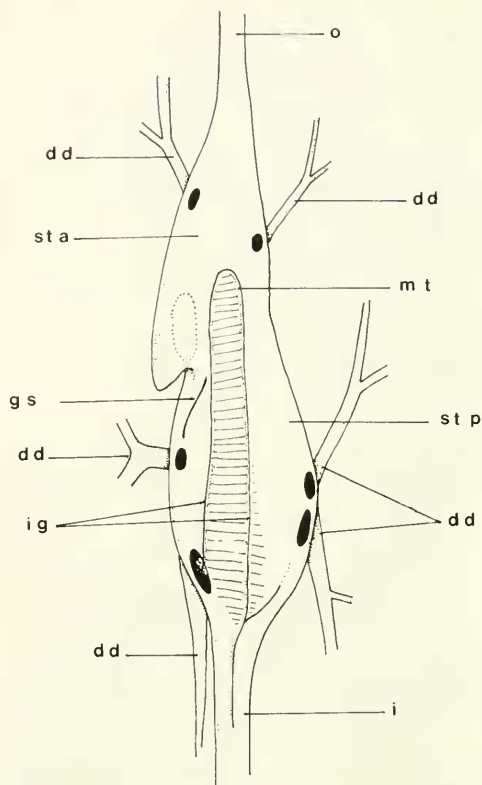
FIG. 11. Dorsal view of stomach with the dorsal wall removed, showing the openings of digestive ducts and the major typhlosole and intestinal groove.

mussels and occasionally probing them. Rhoads *et al.* (1982) considered these crabs to be the most likely predators on the mussels. They found that shells often show repaired damage, especially in the region of the byssal notch. They suggested that mussels shorter than 2.0 cm are usually consumed if attacked. Unsuccessful predator attacks appear to be most frequent in mussels of shell lengths between 2.0 and 5.5 cm while larger mussels appear to be ignored.

About one third of the preserved mussels examined contained the polynoid polychaete *Branchipolynoe symmytilida* (Pettibone, 1984). The worms occurred in the mantle cavity, usually in the posterior region. The gills of specimens with these polychaetes were often thickened and uneven, possibly due to disturbance by the worms. Not all mussels with deformed gills had worms at the time of collections, nor were the gills deformed in all specimens with worms inside. *In situ* TV tape photography shows a live red polychaete leaving a mussel and swimming out of view as the mussel was being collected by R/V *Alvin*'s mechanical arm. Other polychaetes of apparently the same kind are seen swimming freely and crawling over the exterior of the mussels.

Krantz (1981) has described a new and unusual species of predatory mite recovered from detritus associated with a sample of mussels.

Juveniles may reach a length of 27 mm in 294 days or less. Growth rates appear to be influenced mainly by food concentration. Mussels in dense populations close to the vents where there was a high density of microbial food grew two or three times faster than those in peripheral locations where density of microbial food was less.

Growth rings in different individuals could be tentatively correlated at the "Rose Garden" site, indicating synchronous change in mussel growth, possibly in response to change in temperature and nutrient conditions. If such thermal pulsing occurs, it may serve as a cue for gonad development or spawning. As noted above, all of the mussels examined in our study had gonads in regressed condition, which also implies synchrony of the gametogenic cycle.

Interactions with other species. TV tape recorded the brachyuran crab, *Bathograea thermydron* (Williams, 1980) crawling over

DISCUSSION

Shell form and structure of *Bathymodiolus thermophilus* are typical of the Mytilidae, most closely resembling *Modiolus.* The anatomy also conforms generally with that of the Mytilidae but there are several features, though common within the family, which are not found in *Modiolus,* and others that are unique. In the former category are the internal diaphragm within the excurrent siphon (as in *Mytilus* White, 1937; *Lithophaga* and *Leiosolenus* Wilson, 1979, *Botula* Wilson & Tait, 1984) and the divided incurrent and excurrent siphons (as in *Botula* Wilson & Tait, 1984).

The enlarged auricles with a second opening into the longitudinal vein between the two bundles of the posterior byssal retractor muscles and the very small, tubular kidney are unique features of the anatomy.

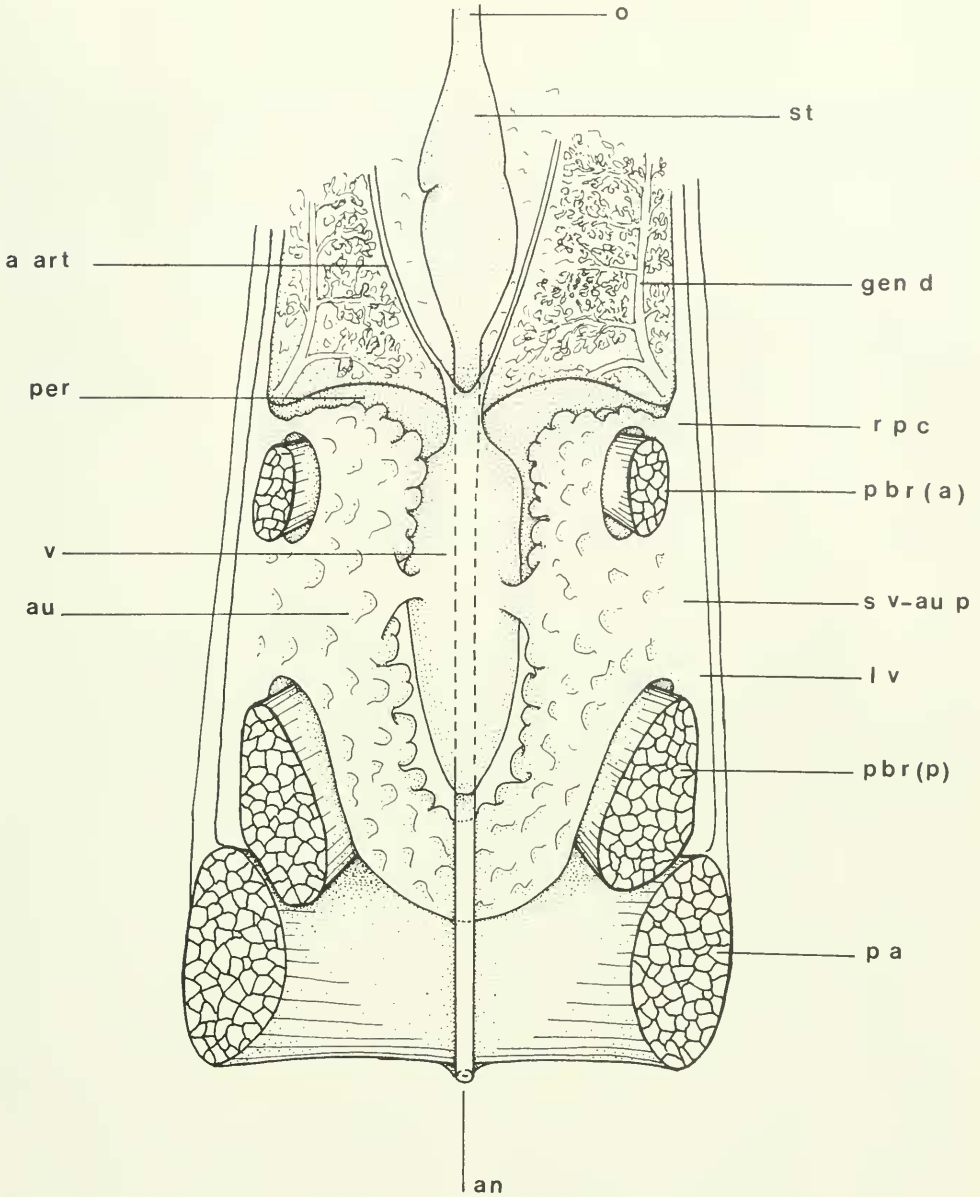The most obvious and remarkable feature

FIG. 12. Dorsal view of the heart showing the narrow anterior connection of the auricles with the longitudinal vein through the reno-pericardial channel, and the wide secondary connection between the anterior and posterior bundles of the posterior byssal retractor muscles.

of this mussel is the extent of ventral fusion of the mantle lobes. It is achieved by normal fusion of the inner folds anteriorly, but posteriorly it is achieved by extraordinary development of the valvular siphonal membrane. This structure is represented in some other mytilids by a thin, transverse, oblique partition from the antero-ventral edge of the branchial septum, partly occluding the incurrent aperture (see Yonge, 1955; *Botula* Wilson & Tate, 1984, fig. 3). In this case the postero-ventral part of the mantle cavity is enclosed by the valvular siphonal membrane except for the short central byssal-pedal gape. Neverthe-

FIG. 13. Photograph of living mussels *in situ*; R–V *Alvin* Dive 885, courtesy of Dr. Robert Hessler.

less the free edges of the inner folds postero-ventrally are extensible and, judging from photographs of the animal in life (Fig. 13), must channel water along the ventral side of the body to that gape.

The gills of *Bathymodiolus*, also, are anomalous among mytilids for which gill structure is known. Although they have the typical 'W' shape, the gills are unusually thick and lack food grooves at the ventral edges of the demibranchs. Perhaps the deep grooves at the free edges of the ascending lamellae are functional food grooves but even in that case the conclusion is inescapable that this mussel does not filter suspended particles in the usual mytilid way.

Further evidence for a different feeding mechanism is found in the alimentary tract of *Bathymodiolus*. The short, direct gut lacking a recurrent loop and the internal structure of the stomach are quite unlike those of any other mytilid so far described. In *Mytilus* (Graham, 1949; Owen, 1955), *Modiolus* (Nelson, 1918; Reid,1965; Morton, 1977), *Leiosolenus* (Purchon, 1957, *Adula* (Fankboner, 1971) and *Musculista* (Morton, 1974) the stomach is a tumid, two-chambered organ with a deep antero-ventral sorting caecum and a prominent left pouch and dorsal hood posteriorly. But in *Bathymodiolus* the stomach is elongate, there is a small lateral pouch on the left side of the anterior chamber but no deep sorting caecum, and a left pouch of the posterior chamber is lacking. In those genera the major typhlosole originates in the caecum but in *Bathymodiolus* it originates on the ventral floor of the anterior chamber and runs straight down the mid-line to the entrance of the intestine. In other genera the intestinal groove originates in the posterior left pouch and curves around the posterior chamber into the sorting caecum of the anterior chamber on the left side of the major typhlosole. In *Bathymodiolus* it originates in the posterior digestive gland duct on the left side and runs straight forward along the left side of the major typhlosole, curves around its anterior end and returns down its right side to the entrance of the intestine. The transverse plications on the floor of the stomach between the two arms of the intestinal groove are not matched by any similar structures in other mytilids. Finally, in the other mytilid genera specified above the ducts of the digestive gland are numerous and asymmetrically grouped, while in *Bathymodiolus* there are

three distinct pairs which enter the stomach laterally.

Although the presence of a crystalline style, gastric shield and plications on the stomach floor confirm that the stomach of *Bathymodiolus* is a particle-sorting chamber, it has a much more simple structure and organization than the stomachs of other mytilids which are extremely complex. If simplicity indicates primitiveness then it can be concluded that *Bathymodiolus* has a primitive gut. The disposition of the paired and separate digestive ducts also may be regarded as primitive (Purchon, 1957).

From these observations it is evident that the water circulation system within the mantle cavity, the capture and carriage of particles on the gills, and the sorting processes within the gut of *Bathymodiolus thermophilus* are atypical of the Mytilidae and that feeding in this species must differ from the usual.

High concentrations of chemoautotrophic, sulphur-oxidizing bacteria occur in the sulphur-rich water in the vicinity of the hydrothermal vents (Corliss *et al.*, 1979; Galápagos Biology Expedition Participants, 1979). These bacteria could be food for the filter-feeding animals living there (Jannasch & Wirsen, 1979; Rau & Hedges, 1979; Karl *et al.,* 1980; Williams *et al.,* 1981). Suspensory feeding on such high concentrations of suspended bacteria might indeed involve mechanisms different from the usual ones.

There is also evidence that *Bathymodiolus* may obtain some or all of its nutrients through symbiosis with sulphur-oxidizing bacteria in the gills. Cavanaugh *et al.* (1981) discovered prokaryotic cells in the trophosome of the vestimentiferan tubeworm *Riftia pachyptila* Jones. Felbeck (1981) demonstrated the presence of sulphur-oxidizing and Calvin-Benson cycle enzymes in that organism, suggesting that sulphur-oxidizing bacteria exist in a symbiotic relationship with it. Subsequently Felbeck *et al.* (1981) have shown that the vent clams *Calyptogena pacifica* Dall and *C. magnifica* Boss & Turner (1980), and the mussel described here, also show evidence of sulphur-oxidizing enzyme activity in the gill tissues. They suggested that these bivalves inhabiting the sulphide-rich environments of the hydrothermal vents "are not only able to tolerate these toxic habitats, but in addition are capable of exploiting the energy of sulphide to drive net CO_2 fixation and, thereby, reduce their dependence on ingestion of

photosynthetically fixed carbon." The simple structure of the gills, labial palps and alimentary tract in *Bathymodiolus* is quite consistent with this possibility. Nevertheless, the anatomical evidence indicates some degree of ciliary feeding on suspended particles, probably bacteria.

Nutrition based on symbiotic sulphur-oxidizing bacteria is now described for several bivalves that live in sulphide-rich environments (Reid & Bernard, 1980; Cavanaugh, 1983; Felbeck, personal communication). In discussing such symbioses in marine invertebrates, Reid & Bernard (1980) commented on the need for a burrow or tube in pogonophorans "to contain and confine the related organisms and prevent the dissipation of useful solutes." The extreme degree of ventral mantle fusion in *Bathymodiolus* may also serve this function.

In several of the preserved specimens, small particles of bright yellow particulate matter, presumed to be elemental sulphur, were observed trapped in mucus on the gills. Jones (1981) made a similar observation in *Riftia.* One might expect that an animal living in such a toxic environment would have a specially efficient excretory system. It is surprising, therefore, to find that the kidney in *Bathymodiolus* is so small. The vascular system, on the other hand, is unusually well developed. The clue to interpretation of these unusual structures may lie in the physiology of nutrition based on suspended or symbiotic sulphur-oxidizing bacteria, or in the mussels' physiological tolerance to the sulphur-rich environment.

The phylogenetic affinities of *Bathymodiolus* remain problematical. The similarity of the modioliform shell to that of *Modiolus* is clearly a case of parallelism for the anatomical characters are very different. The extent of mantle fusion, the simple gut, the lack of ventral food grooves on the gills, the small kidney and the large auricles with second connections to the longitudinal veins, are all characters which have not been previously described in the Mytilidae. The physiological implications of these features indicate a different life-style and evolutionary origins to the Mytilinae, Modiolinae, Lithophaginae, Crenellinae or Musculininae. We confidently introduce the new subfamily Bathymodiolinae for this new genus and species.

There are several small, modioliform mytilids in the Pacific region. Knudsen (1970) described *Modiolus abyssicola* (Fig. 14B)
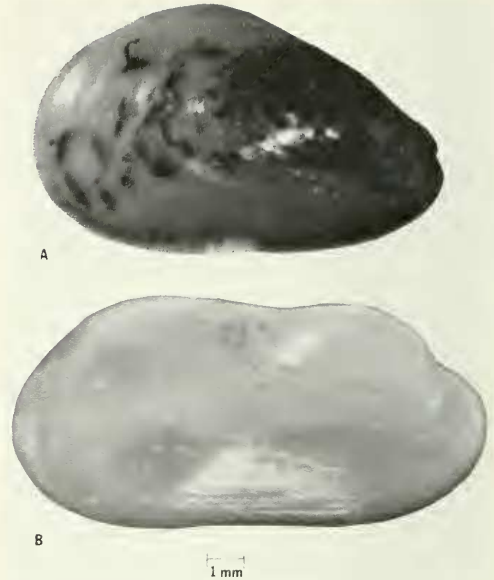
FIG. 14. A. Small specimen of *Bathymodiolus thermophilus.* B. Holotype of *Modiolus aybssicola* Knudsen.

from 3670–3270 m in the Gulf of Panama (5°49′N, 78°52′W). This small mussel (max. length recorded 17.2 mm) has an arcuate modioliform shell similar to that of a medium to large-sized *Bathymodiolus thermophilus* although juvenile specimens of the latter are not arcuate (Fig. 14A). Because of this similarity and the proximity of the localities, early consideration was given to the possibility that the large mussels from the hydrothermal vents might be adults and the Panama ones juveniles of one species. Independently we have examined the anatomy of preserved specimens in the type-series of *M. abyssicola,* through the courtesy of Dr. Knudsen. The posterior retractors of this species are divided but there is no siphonal development, the branchial septum is short and simple, there is a large incurrent aperture (gape) from the ventral side of the branchial septum to the anterior adductor, and the intestine is short but looped as in *Modiolus.* Gonads, gonoducts and a prominent gonad aperture were observed in the larger specimens, dispelling any suggestion that these are juveniles. For these reasons, we conclude that *M. abyssicola* may be a true *Modiolus* or at least a modiolinid, and the possibility of a relationship with the species described here can be rejected.

Modiolus projectus Verco, 1908, from 200

fathoms off South Australia is another small species (holotype length 10.9 mm) of similar form. It is characterized by a conspicuous "projecting lamina" below the ligament. The generic affinities of this species remain undetermined but this unusual character makes a relationship with *Bathymodiolus* improbable.

Adipicola Dautzenberg, 1927, is a genus containing several small deep water modioliform mytilids. The prosogyrate umbos are situated well back from the anterior end and there is an anterior (lunular) keel as well as a posterior one. A sub-ligamental ridge is lacking, and the ligamental plate, though more or less vertical posteriorly, curves under the margin near the umbos. In *A. simpsoni* (Marshall, 1900) and *A. argenteus* (Jeffreys, 1876) there are pseudo-taxodont teeth or denticles on the dorsal margin beneath and behind the ligament; these are lacking in the type-species *A. pelagica* (Woodward, 1854). The anatomy of these species is unknown to us although the posterior retractor muscle scars are not divided in *A. simpsoni* at least. The Pacific genus *Terua* Dall, Bartsch & Rehder, 1938, appears to be very close to *Adipicola*. The type-species *T. pacifica* Dall, Bartsch & Rehder, 1938, and *T. japonica* (Habe, 1971) also have hinge denticles. Dried specimens of the latter species in the USNM (204525) show a long ventral gape, no excurrent siphon, and undivided posterior retractor muscles. This complex of small modioliform mytilids is in need of revision. In the meantime, even in the absence of much information about their anatomy, we are confident that they are not closely related to the new species from the Galapagos hydrothermal vents. Nevertheless, an affinity for *Bathymodiolus* might eventually be established in this direction.

LITERATURE CITED

ATKINS, D., 1937, On the ciliary mechanisms and interrelationships of the lamellibranchs. Part III. Types of lamellibranch gills and their food currents. *Quarterly Journal of Microscopical Science*, 79: 375–421.

BALLARD, R. D. & GRASSLE, J. F., 1979, Return to oases of the deep. *National Geographic*, 156: 689–705.

BOSS, K. J. & TURNER, R. D., 1980, The giant white clam from the Galapagos Rift, *Calyptogena magnifica* species novum. *Malacologia*, 20: 161–194.

BOTTJER, D.J. & CARTER, J. G., 1980, Functional and phylogenetic significance of projecting periostracal structures in the Bivalvia (Mollusca). *Journal of Paleontology*, 54: 200–216.

BURRESON, E. M., 1981, A new deep-sea leech, *Bathybdella sawyeri*, n. gen., n. sp., from thermal vent areas on the Galapagos Rift. *Proceedings of the Biological Society of Washington*, 94: 483–491.

CAVANAUGH, C. M., 1983, Symbiotic chemotrophic bacteria in marine invertebrates from sulphur-rich habitats. *Nature*, 302: 58–61.

CAVANAUGH, C. M., GARDINER, S. L., JONES, M., JANNASCH, H. W. & WATERBURY, J., 1981, Prokaryotic cells in the hydrothermal vent tube worm *Riftia pachyptila* Jones: possible chemoautotrophic symbionts. *Science*, 213: 340–342.

CORLISS, J. B. & BALLARD, R. D., 1977, Oases of life in the cold abyss. *National Geographic*, 152: 441–453.

CORLISS, J. B., DYMOND, J., GORDON, L. I., EDMOND, J. M., VON HERZEN, R. P., BALLARD, R. D., GREEN, K., WILLIAMS, D., BAINBRIDGE, A., CRANE, K. & VAN ANDEL, T. H., 1979, Submarine thermal springs on the Galapagos Rift. *Science*, 203: 1073–1083.

DESBRUYÈRES, D., CRASSOUS, P., GRASSLE, J., KHRIPOUNOFF, A., REYSS, D., RIO, J. &

VAN PRAET, M., 1982, Données ecologiques sur un nouveau site d'hydrothermalisme actif de la ride du Pacifique oriental. *Comptes Rendus des Séances de l'Académie des Sciences* [Paris], ser. III, Sciences de la Vie 295: 489–494.

DESBRUYÈRES, D. & LAUBIER, L., 1982, *Paralvinella grasslei,* new genus, new species of Alvinellinae (Polychaeta: Ampharetidae) from the Galápagos Rift geothermal vents. *Proceedings of the Biological Society of Washington,* 95: 484–494.

EDMOND, J. M., 1982, Ocean hot springs: a status report. *Oceanus,* 25: 22–27.

ENRIGHT, J. T., NEWMAN, W. A., HESSLER, R. R. & McGOWAN, J. A., 1981, Deep-ocean hydrothermal vent communities. *Nature,* 289: 219–220.

FANKBONER, P. V., 1971, The ciliary currents associated with feeding, digestion, and sediment removal in *Adula* (*Botula*) *falcata* Gould, 1851. *Biological Bulletin,* 140: 28–45.

FELBECK, H., 1981, Chemoautotrophic potential of the hydrothermal vent tube worm, *Riftia pachyptila* Jones (Vestimentifera). *Science,* 213: 336–338.

FELBECK, H., CHILDRESS, J. J. & SOMERO, G. N., 1981, Calvin-Benson cycle and sulphide oxidation in enzymes in animals from sulphide-rich habitats. *Nature,* 293: 291–293.

FRETTER, V., GRAHAM, A. & McLEAN, J. H., 1981, The anatomy of the Galapagos Rift limpet, *Neomphalus fretterae. Malacologia,* 21: 337–361.

GALÁPAGOS BIOLOGY EXPEDITION PARTICIPANTS, 1979, Galapagos '79: initial findings in a deep-sea biological quest. *Oceanus,* 22(2): 2–10.

GRAHAM, A., 1949, The molluscan stomach. *Transactions of the Royal Society of Edinburgh,* 61: 737–776.

JANNASCH, H. W. & WIRSEN, C. O., 1979, Chemosynthetic primary production at East Pacific sea floor spreading centers. *Bioscience,* 29: 592–598.

JONES, M., 1981, *Riftia pachyptila* Jones: observations on the vestimentiferan worm from the Galapagos Rift. *Science,* 213: 333–336.

KARL, D. M., WIRSEN, C. O. & JANNASCH, H. W., 1980, Deep-sea primary production at the Galapagos hydrothermal vents. *Science,* 207: 1345–1347.

KNUDSEN, J., 1970, The systematics and biology of abyssal and hadal Bivalvia. *Galathea Report* 11: 1–241.

KRANTZ, G. W., 1981, *Copidognathus papillatus,* a new species (Acari: Actinedida: Halacaridae) from the Galápagos Rift, Pacific Ocean. *Canadian Journal of Zoology,* 60: 1728–1731.

LAUBIER, L. & DESBRUYÈRES, D., 1984, Les oasis du fond des océans. *La Recherche,* 15: 1506–1517.

LE PENNEC, M., LUCAS, A. & PETIT, H., 1984 ["1983"], Études préliminaires sur un Mytilidae des sources hydrothermales du Pacifique. *Haliotis,* 13: 69–82.

LONSDALE, P., 1977, Clustering of suspension-feeding macrobenthos near abyssal hydrothermal vents at oceanic spreading centers. *Deep-Sea Research,* 24: 857–863.

LUTZ, R. A., JABLONSKI, D., RHOADS, D. C. & TURNER, R. D., 1980, Larval dispersal of deep-sea hydrothermal vent bivalve from the Galapagos Rift. *Marine Biology,* 51: 127–133.

McLEAN, J. H., 1981, The Galapagos Rift limpet *Neomphalus:* relevance to understanding the evolution of a major Paleozoic-Mesozoic radiation. *Malacologia,* 21: 291–336.

MORTON, B., 1974, Some aspects of the biology, population dynamics, and functional morphology of *Musculista senhausia* Benson (Bivalvia, Mytilidae). *Pacific Science,* 28: 19–33.

MORTON, B., 1977, The biology and functional morphology of *Modiolus metcalfei* (Bivalvia: Mytilacea) from the Singapore mangrove. *Malacologia,* 16: 501–517.

NELSON, T. C., 1918, On the origin, nature and function of the crystalline style of lamellibranchs. *Journal of Morphology,* 31: 53–111.

NEWMAN, W. A., 1979, A new scalpellid (Cirripedia); a Mesozoic relic living near an abyssal hydrothermal spring. *Transactions of the San Diego Society of Natural History,* 19: 153–167.

OCKELMANN, K. W., 1983, Descriptions of mytilid species and definition of the Dacrydiinae n. subfam. (Mytilacea-Bivalvia). *Ophelia,* 22: 81–123.

OWEN, G., 1955, Observations on the stomach and digestive diverticulae of the Lamellibranchia I. The Anisomyaria and Eulamellibranchia. *Quarterly Journal of Microscopical Science,* 96: 517–537.

PETTIBONE, M. W., 1984, A new scale-worm commensal with deep-sea mussels on the Galapagos hydrothermal vent (Polychaeta: Polynoidae). *Proceedings of the Biological Society of Washington,* 97: 226–239.

PURCHON, R. D., 1957, The stomach in the Filibranchia and Pseudolamellibranchia. *Proceedings of the Zoological Society of London,* 129: 27–60.

RAU, G. H. & HEDGES, J. I., 1979, Carbon-13 depletion in a hydrothermal vent mussel: suggestion of a chemosynthetic food source. *Science* 203: 648–649.

REID, R. G. B., 1965, The structure and function of the stomach in bivalved molluscs. *Journal of Zoology, London.* 147: 156–184.

REID, R. G. B. & BERNARD, F. R., 1980, Gutless bivalves. *Science,* 208: 609–610.

RHOADS, D. C., LUTZ, R. A., CERRATO, R. M. & REVELAS, E. C., 1982, Growth and predation activity at deep-sea hydrothermal vents along the Galapagos Rift. *Journal of Marine Research,* 40: 503–516.

RHOADS, D. C., LUTZ, R. A., REVELAS, E. C. & CERRATO, R., 1981, Growth of bivalves at deep-sea hydrothemal vents along the Galapagos Rift. *Science,* 214: 911–913.

RISE PROJECT GROUP: SPIES, F. N., MacDONALD, K. C., ATWATER, T., BALLARD, T., CARRANZA, A., CORDOBA, D., COX, C., DIAZ

GARCIA, V. M., FRANCHETEAU, J., GUER-
RERO, J., HAWKINS, J., HAYMON, R., HES-
SLER, R., JUTEAU, T., KASTNER, M., LAR-
SON, R., LUYENDYK, B., MacDOUGALL, J. D.,
MILLER, S., NORMARK, W., ORCUTT, J. &
RANGIN, C., 1980, East Pacific Rise: hot springs
and geophysical experiments. *Science,* 207:
1421–1433.

SOOT-RYEN, T., 1955, A report on the family
Mytilidae (Pelecypoda). *Allan Hancock Pacific
Expeditions,* 20(1): 1–175.

WHITE, K., 1937, *Mytilus. Liverpool Marine Biology
Committee Memoirs,* 31: 1–117, 10 pl.

WILLIAMS, A. B., 1980, A new crab family from the
vicinity of submarine thermal vents on the Gala-
pagos rift (Crustacea: Decapoda: Brachyura).
*Proceedings of the Biological Society of Wash-
ington,* 93: 443–472.

WILLIAMS, A. B. & CHACE, F. A., 1982, A new
caridean shrimp of the family Bresiliidae from
thermal vents of the Galapagos Rift Zone, East
Pacific. *Journal of Crustacean Biology,* 2: 136–
147.

WILLIAMS, P. M., SMITH, K. L., DRUFFEL, E. M. &
LINICK, T. W., 1981, Dietary carbon sources of
mussels and tubeworms from Galapagos hydro-
thermal vents determined from tissue $_{14}$C activ-
ity. *Nature,* 292: 448–449.

WILSON, B. R., 1979, A revision of Queensland
lithophagine mussels (Bivalvia: Mytilidae:
Lithophaginae). *Records of the Australian
Museum,* 32: 435–489.

WILSON, B. R. & TAIT, R., 1984, Systematics,
anatomy and boring mechanisms of the rock-
boring mytilid bivalve *Botula. Proceedings of the
Royal Society of Victoria,* 96: 113–125.

YONGE, C. M., 1955, Adaptation to rock-boring
Botula and *Lithophaga* (Lamellibranchia, Mytili-
dae) with a discussion of the evolution of this
habit. *Quarterly Journal of Microscopical Sci-
ence,* 96: 383–410.

YONGE, C. M., 1957, Mantle fusion in the Lamelli-
branchia. *Pubblicazioni della Stazione Zoologica
di Napoli,* 29: 15–171.

NOTE

The following appeared while this paper was in
press (see also p. 255, footnote 3):

FIALA-MEDIONI, A., 1984, Mise en évidence par
microscopie électronique à transmission de
l'abondance de bactéries symbiotiques dans la
branchie de Mollusques bivalves de sources
hydrothermales profondes. *Comptes Rendus de
l'Académie des Sciences* [Paris], III, 298: 487–
492, 2 pl.

LE PENNEC, M. & PRIEUR, D., 1984, Observa-
tions sur la nutrition d'un Mytilidae d'un site
hydrothermal actif de la dorsale du Pacifique.
Ibid., 298: 493–498, 1 pl.

ED.